Does the sociality of pollinators shape the organisation of pollination networks?

Abstract

A striking structural pattern of pollination networks is the presence of a few highly connected species which has implications for ecological and evolutionary processes that create and maintain diversity. To understand the structure and dynamics of pollination networks we need to know which mechanisms allow the emergence of highly connected species. We investigate whether social pollinator species are highly connected in pollination networks, and whether network structure is affected by the presence of high proportions of social pollinator species. Social insects are abundant, with long activity periods and, at the highest level of social organisation, specialised foraging castes. These three attributes are likely to increase the number of interactions of social species and, consequently, their role in pollination networks. We find that social species have, on average, more prominent network roles than solitary species, a possible mechanism being the individual-rich colonies of social insects. However, when accounting for the shared evolutionary history of pollinators, sociality is only associated with highly interactive roles in Apidae. For apid bees, our structural equation analysis shows that the effect of sociality on species network roles is an indirect result of their high levels of interaction frequency. Despite the relative importance of sociality at a species-level, an increasing proportion of social species in pollination networks did not affect overall network structure. Our results suggest that behavioural traits may shape patterns of interaction of individual species but not the network-level organisation of species interactions. Instead, network structure appears to be determined by more general aspects of ecological systems such as interaction intimacy, patterns of niche overlap, and species abundance distributions.

Keywords: betweenness; centralisation; centrality; closeness; ecological networks; weighted modularity; mutualism; weighted nestedness; species roles; sociality

Introduction

Interactions between assemblages of plants and pollinators are organised as networks of interacting species. The structure of these networks may have implications for species coexistence (Bascompte et al. 2006), maintenance of species diversity (Thébault and Fontaine 2010), and coevolutionary dynamics (Guimarães et al. 2017). One of the most conspicuous structural patterns in complex networks (Barabási and Albert 1999) is the large variation in the number of interactions among component species (Jordano et al. 2003, Vázquez and Aizen 2004). This large variation is due to the fact that a few species are highly connected, interacting with several species, whereas most species have few interactions. Highly connected species may be important to community functioning as they connect otherwise isolated modules, i.e. subgroups of interacting species, thereby decreasing network modularity (Olesen et al. 2007). They form the network core and generate the skewed interaction structure of mutualistic networks which leads to nestedness (Bascompte et al. 2003). Highly connected species may also mediate evolution and coevolution in mutualistic networks, favouring complementarity and convergence of traits (Guimarães et al. 2011). Given the relevance of highly connected species to ecological and evolutionary processes shaping communities, it is crucial to identify traits which allow the emergence of these lifestyles that depend upon a diversity of mutualistic partners to persist (Thompson 2005).

Network interaction patterns are ultimately determined by the attributes of interacting species such as abundance (Vázquez et al. 2009), phenology (Vázquez et al. 2009; Martín González et al. 2012; Vizentin-Bugoni et al. 2014), morphology (Stang et al. 2006; Martín González et al. 2012; Vizentin-Bugoni et al. 2014) and potentially behaviour. Various lines of evidence, including the fitting of assembly models to

empirical data (Pires et al. 2011), the analysis of network dimensionality (Eklöf et al. 2013), and the study of traits that constrain the occurrence of interactions ("forbidden links", Olesen et al. 2011), suggest a few statistically independent traits are crucial to our understanding of the organisation of ecological networks.

Social insect species are defined as species presenting some level of social organisation, ranging from females that nest together to highly eusocial species with overlapping adult generations, cooperative brood care and reproductive division of labour (Wilson 2000). Several studies found that social pollinators, such as honeybees (*Apis* spp.) and bumblebees (*Bombus* spp.), are among the main floral visitors in pollination networks. This was due to their high levels of interaction frequency (Vázquez and Aizen 2003, Memmott et al. 2004, Olesen et al. 2007, Forup et al. 2008), and potential to affect overall community organisation and network robustness (Giannini et al. 2015, Traveset et al. 2017).

The prominent role of social pollinators in ecological networks is hypothesised to be associated with three aspects of sociality Thompson (1982). First, colonies of social insects are generally composed of many individuals, and in mutualistic assemblages, abundant species often have a high number of interactions (Krishna et al. 2008, Fort et al. 2016). We emphasise that, although the number of colonies defines the number of reproductive individuals in a population of social species, in the context of plant-insect interactions - where individuals are the interactive entities - the number of individuals is a more accurate measure of abundance. Second, colonies of many social insects are active throughout the flowering season (Michener 2007), increasing the opportunity for interaction with many phenologically scattered plant species. Indeed, the number of interactions that pollinator species establish in pollination networks varies with the length of their activity period (Olesen et al. 2008). Over a longer

timescale, social insects may connect temporally isolated subgroups of species from different years or seasons, including pollinators with short life spans or plants with short flowering periods. Third, the presence of foraging castes in some social species may favour the establishment of interactions with a greater number of plant species, as these individuals are able to dedicate more of their time to foraging and recruiting foragers. This is in contrast to solitary species which are required to multi-task. Indeed, social bee species with group foraging behaviour and large colony sizes have been known to dominate floral resources and displace other species of floral visitor (Lichtenberg et al. 2010). In summary, sociality might favour pollinator importance through their abundance, their long periods of activity and division of labour.

Network analysis is able to identify highly connected species in ecological assemblages, quantify their effect on the overall network structure and shed light on traits that promote these relevant ecological roles. For instance, species network roles can be described by centrality metrics, which measure species influence on the network structure. Species with high centrality greatly contribute to network organisation as they are at short distances - measured in number of interactions - to other species in the network, are frequently in between other species' shortest distances, and are connected to other species by multiple indirect pathways. Thus, centrality metrics can identify the most topologically important species for network structure and robustness (Martín González et al. 2010, Vidal et al. 2014). Network metrics can be also related to species functional roles and, consequently to community functioning. Coux et al. (2016) found that locally highly connected pollinators had traits sufficiently similar to the average traits of the pollinator assemblage, allowing them to visit several plant species, whilst still having sufficiently exclusive traits to avoid competition (see Ruggera et al. 2016 for an example from seed-dispersal networks).

Recent studies on the structure of pollination networks, which included networks composed exclusively of social pollinators, have suggested that sociality might affect the structure of these systems (Santos et al. 2010, Mello et al. 2011, Zotarelli et al. 2014). The next step is to investigate how sociality shapes the structure of pollination networks at a species and at a network level, and across multiple networks. Here, we investigate whether sociality shapes the structure of pollination networks by asking: 1) Do network roles of social and solitary pollinator species differ within networks? 2) Do network roles of social and solitary pollinator species differ within Hymenopteran families? 3) Is the structure of pollination networks affected by the presence of high proportions of social pollinator species? We hypothesise that sociality may favour species to become highly connected in pollination networks (Thompson 1982). If this is the case, we expect that a large representation of social insect species can shape the overall structure of pollination networks in predictable ways. We anticipate that a high proportion of social pollinators within networks decreases distances between species, both by direct and indirect interactions, and increases interaction overlap between species. These highly connected social species would also connect isolated groups of species.

Materials and Methods

We analysed 29 published quantitative pollination networks, i.e. with information on the frequency of interactions between plant and pollinator species (Fig. 1, Supplementary material Appendix 1, Table A1). In most studies, interaction frequency is expressed as the number of insect individuals observed visiting a plant species. In the case of social species, the insect individual was likely to be a worker. Even if it is known that not all visitation events result in pollination and some cheating

occurs (Genini et al. 2010), we nevertheless refer to our networks as pollination networks, as cheating is an integral part of pollination systems. Cheaters have evolved and are able to persist due to the existence of plant-pollinator mutualisms and are likely to affect the ecology and evolution of the system. We therefore refer to all insects as flower visitors hereafter. All studied networks include both solitary (from several orders, frequently including Hymenoptera) and social species (bees, wasps and ants). All species were included in the calculations of network metrics (see *Species roles* and *Network structure*).

Species roles

We quantified the network roles of all flower visitor species integrating networks using three species-level qualitative metrics that do not account for frequency of interactions between species: degree, closeness and betweenness centrality (Supplementary material Appendix 1, Eq. A1 to A3). The degree is the number of links per flower visitor species, i.e. the number of plant species each flower visitor species interacts with. Both closeness and betweenness centrality are measured from a unipartite projection of a bipartite network, i.e. flower visitors are connected when they share plant species. Closeness centrality is the mean shortest distance (measured in number of interactions) to all other flower visitors in the network, while betweenness centrality is the proportion of shortest distances connecting pairs of flower visitor species that cross a focal flower visitor species (Martín González et al. 2010). Both centrality metrics describe the position of a given species in the network, specifically, its proximity to other species (closeness centrality) and its role as a potential bridge between species (betweenness centrality). Therefore, central species are likely to efficiently spread ecological disturbance (Gómez et al. 2013) and selective pressures

(Guimarães et al. 2017) through the network.

We additionally used four quantitative metrics in which interaction frequency was taken into account: interaction strength, among-module connectivity, standardised within-module strength and weighted centrality (Supplementary material Appendix 1, Eq. A4 to A8). Interaction strength is the sum of the dependences every plant species has on a focal flower visitor species and its value increases both with the number of plant species visited and with the frequency of visits (Bascompte et al. 2006). Among-module connectivity describes how important species are in connecting distinct modules and standardised within-module strength describes how important species are in connecting species within their own module (Olesen et al. 2007). In weighted centrality, a weighted index based on Katz centrality, a species is central not because it is closer to other species but because multiple direct and indirect pathways connect it to disparate species in networks (see for example Guimarães et al. 2017). The quantitative metrics complement our qualitative analysis by incorporating the differences in frequency of interactions across flower visitor species of different levels of sociality. We assume that potential sampling bias across different species is not correlated with sociality.

Despite describing different network roles played by species in pollination networks, several of our species-level metrics were highly correlated (Supplementary material Appendix 1, Table A3). We therefore used principal component analysis (PCA, following Sazima et al. 2010) to summarise the information of our seven metrics into two variables. PCA was performed using the log-transformed values of degree, interaction strength and weighted centrality, and the log(x+1)-transformed values of among-module connectivity, closeness and betweenness centrality. Together, the first and second principal components explain 72.8% of the variation in our data

(PC1=55.1% and PC2=17.7%). PC1 is positively correlated with all metrics but most strongly with degree, interaction strength and weighted centrality (Supplementary material Appendix 1, Table A4). Therefore, species with high PC1 values are highly interactive species on which several plants species are highly dependent upon and are connected to other species in the network also by multiple indirect pathways. In contrast, PC2 is only highly correlated with closeness centrality (Supplementary material Appendix 1, Table A4). Therefore, species with high PC2 values are at short distances to other flower visitors in the network.

Network structure

We characterised network structure using metrics which may be affected by the presence of highly connected species: weighted nestedness, closeness and betweenness centralisation (both unweighted) and weighted modularity (Supplementary material Appendix 1, Eq. A9 to A13). Nestedness is a pattern in which specialist species interact with a subset of the species with which highly-connected species interact (Almeida-Neto and Ulrich 2011). Highly connected species may also generate networks with high centralisation - a network-level pattern associated with the presence of a few species with high centrality while most species have low centrality. The two indexes of network centralisation (closeness and betweenness) are based on unipartite projections in which two flower visitors are connected if they share at least one plant partner. Networks have high closeness centralisation if there is a large variation in the length of shortest distances connecting pairs of flower visitors in the network, so that few visitors are much closer to the rest of the network than most species. Networks have high betweenness centralisation if there is a large variation in how frequently flower visitors are in-between the shortest distances connecting pairs of other visitors, so that only a

few species are constantly in-between other species' shortest distances (de Nooy et al. 2005). Modularity quantifies the number and the level of isolation of network modules. Networks are modular if sets of species interact more among themselves than with species in other sets (Olesen et al. 2007). We used the NODF-Program to quantify weighted nestedness with wNODF (Almeida-Neto and Ulrich 2011), the R package "bipartite" (R Core Team 2014) to calculate closeness and betweenness centralisation (Freeman 1979, de Nooy et al. 2005), and to calculate the bipartite measure of modularity Q (Barber 2007) in weighted networks with the algorithm DIRTLPAwb+ (Beckett 2016).

Sociality

Only hymenopteran species were included hereafter, even if we characterised the network roles of all flower visitor species, to ensure that the species included in the statistical analysis were broadly comparable. We assigned each hymenopteran species to one of four categories, representing decreasing level of sociality: highly eusocial (E), primitively eusocial (P), communal (C) and solitary (S) (Michener 2007, Supplementary material Appendix 1, Table A2). Eusocial species show cooperative behaviour in the care of their young, as well as division of labour, an overlap of generations (Wilson 2000) and, in most cases, perennial colonial activity (Michener 2007). Non-perennial species which still exhibited one or more of these defining eusocial traits were classified as primitively eusocial (e.g. most *Bombus* spp., Wilson 2000, Michener 2007). Therefore, the main difference between eusocial and primitively eusocial species is the perenniality of eusocial colonies, that require constant food provisioning, which affects patterns of resource use and, consequently, of species interactions. Solitary and communal species were those lacking all three traits defining

eusociality, though females of communal species may still show aggregate nesting (Michener 2007). Species which could not be confidently assigned to one category were excluded from the analysis (Supplementary material Appendix 1, Table A2).

For each network, we computed the proportion of social (including highly eusocial, primitively eusocial, and communal) hymenopteran species, $I_S=(E+P+C)/H$, and the proportion of highly eusocial hymenopteran species, $I_E=E/H$, where H is the number of hymenopteran species in the network. Ants were excluded as they are often poor pollinators (Janzen 1977, Beattie and Hughes 2002). However, using all flower visitors as the denominator instead of just hymenopterans (results not shown), and including ant species as pollinators (Supplementary material Appendix 1, Tables A6-A9) produced qualitatively similar results.

Statistical analysis

Using general linear mixed models (GLMMs), we tested whether sociality is associated with differences in network roles of flower visitor species (species-level metrics summarised into PC1 and PC2). There were four competing models, representing alternative scenarios in which network roles were: 1) not affected by sociality (no fixed effect); 2) affected by sociality (solitary versus all social species - C, P and E - combined); 3) affected by both sociality (same as above) and interaction frequency; and 4) only affected by interaction frequency. Since numerical effects (such as those caused by species abundances and interaction frequencies) are known to affect species roles in ecological networks (Fort et al. 2016), we included interaction frequency as an explanatory variable in models 3 and 4 to separate the effects of sociality on species roles from a simple consequence of their interaction frequencies. Although interaction frequencies are not the same as abundance, they are often

correlated with species abundances and effectively capture the numerical effects of an interaction, i.e. a species is structurally important because it is a frequent interactor (Fort et al. 2016). Network identity was specified as a random effect in all competing models to account for the fact that multiple species belong to the same network. We have also performed the analysis separately for each network to account for the fact that the same species can occur in multiple networks. We used the Akaike Information Criteria (AIC) to select the model that best described species network roles. Akaike Information Criteria combines model likelihood with simplicity in number of parameters to select between candidate models. Since for both PC1 and PC2 a model including sociality (models 3 and 2, respectively) was the most likely (see *Results*), we explored whether the different levels of sociality affect network roles in a second round of analysis. In this round, the selected model competed with an additional model (models 3.b and 2.b, respectively) that had a similar structure to the selected model, but in which sociality was split into its four categories (S, C, P and E).

Ideally, since closely related species share traits other than sociality that may affect their interaction patterns (Rezende et al. 2007a), the effects of shared evolutionary history among species should be controlled by means of phylogenetic comparative methods. However, eusociality evolved just a few times in Hymenoptera (Hughes et al. 2008), strongly limiting the number of independent phylogenetic contrasts. Hence, for each species-rich hymenopteran family encompassing both solitary and social species (Apidae, Halictidae and Vespidae), we performed t-tests to investigate whether social species consistently showed higher mean values for PC1 and PC2 than solitary species. Given the association between sociality and interaction frequency and between interaction frequency and PC1 and PC2 (Fig. 3c-e), for Apidae (the most species-rich family in our dataset) we also performed a structural equation

analysis to separate the direct effect of sociality on PC1 and PC2, from its indirect effect mediated by interaction frequency. For this analysis, values of interaction frequency, PC1 and PC2 were *Z*-scored within each network.

If social flower visitors are in fact highly connected, their larger representation in networks may be expected to increase network centralisation and the overlap in species interactions (increasing nestedness and decreasing modularity). Using general linear models (GLMs), we tested whether the increasing proportion of social (I_S) and highly eusocial (I_E) hymenopteran species in a network was related to increasing nestedness, closeness and betweenness centralisation, and to decreasing modularity. To allow across-network comparisons, we controlled the effects of species richness, connectance and heterogeneity in the number of interactions using null models. For wNODF, we used the null model *rc* (NODF-Program, Almeida-Neto and Ulrich 2011) that distributes interactions in proportion to species interaction frequency until marginal totals are reached. For closeness and betweenness centralisation we distributed interactions in proportions to the mean standardised degree of potentially interacting species (null model 2, Bascompte et al. 2003), and for Q in proportion to species interaction frequency. We generated 1000 null networks (only 100 for wNODF and Q of the four largest networks, Supplementary material Appendix 1, Table A5) to compute *Z*-scores of all metrics. We used AIC to select from three competing models the one that best reproduced each of the network-level metrics: 1) no effect of sociality; 2) proportion of social hymenopteran species (I_S) affects metrics and; 3) proportion of highly eusocial hymenopteran species (I_E) affects metrics.

Results

Mean species richness of flower visitors in the 29 networks was 169.5 ± 226.7

species (mean ± SD, min = 12, max = 878, median = 66). Hymenopterans were, on average, a major component of the networks constituting 28.8% ± 21.9 of the flower visitor assemblage (mean ± SD, min = 5.56%, max = 100%). Among hymenopterans (ants excluded), solitary species made up around half of all species which could be assigned to one of the four categories (50.8% ± 27.7, min = 0%, max = 91.3%), the remainder displaying some level of sociality. Primitively eusocial species made up 17.2% of the total (± 25, min = 0%, max = 100%), followed by highly eusocial (11.7% ± 11.4, min = 0%, max = 40%), and communal (4.5% ± 9.3, min = 0%, max = 33%). All networks were significantly nested (NODF = 16.5 ± 12.9, mean ± SD), but half or less were more centralised (closeness centralisation: 0.03 ± 0.03, betweenness centralisation: 0.23 ± 0.17, mean ± SD), or modular (0.49 ± 0.11, mean ± SD) than expected from the null model (Supplementary material Appendix 1, Table A5).

Social hymenopteran species (C, P and E) had, on average, higher values of PC1 (correlated with degree, interaction strength and weighted centrality) but lower values of PC2 (correlated with closeness centrality) than solitary species (Fig. 2). Both sociality and interaction frequency were positively associated with highly interactive species - those connected to several species in the network by direct and indirect pathways (model 3 was selected for PC1 in the first round of analysis, Table 1). However, these patterns were not affected by increasing levels of sociality (model 3 was again selected in the second round of analysis, Table 1). These results were corroborated by the analysis performed on each network separately. Of the 22 networks (out of 29) with sufficient species for analysis, 19 showed evidence of a positive association between sociality and highly interactive network roles (Supplementary material Appendix 1, Table A7). Surprisingly, we found that sociality was negatively associated with how close (in number of direct interactions) species were to other

species in the network (model 2 was selected for PC2 in the first round of analysis, Table 1). Additionally, species' PC2 scores were better explained by the different classes of sociality than by sociality *per se* (model 2.b was selected in the second round of analysis, Table 1). Nevertheless, the results of the analysis performed on each individual network showed no consistent trend across networks (Supplementary material Appendix 1, Table A8). Thus, our results support a positive association between sociality and interaction frequency with PC1 (hymenopteran species with highly interactive network roles), but do not extend to PC2 (closeness centrality).

A positive effect of sociality on PC1 was also found at the family level for Apidae (Fig. 3a). Social apid bee species had significantly higher PC1 scores than solitary species ($t=4.4$, $df=222.03$, $P<0.001$), indicating that social Apidae species visited a greater number of plant species more frequently and were more connected to other species in the network through indirect pathways than solitary apid bees. However, the structural equation analysis performed for Apidae species indicated that the positive and significant effect of sociality on PC1 was indirect, mediated by species interaction frequency (Fig. 3f), while the direct effect of sociality on PC1 was only marginally significant ($p=0.05$). In Halictidae and Vespidae, there was no effect of sociality on PC1 (Fig. 3a; Halictidae: PC1: $t=0.61$, $df=44.6$, $P=0.54$; Vespidae: $t=1.85$, $df=64$, $P=0.07$). In the three families, social species had lower values of PC2 than solitary species (Fig. 3b; Apidae: $t=2.27$, $df=222.81$, $P=0.02$; Halictidae: $t=2.49$, $df=48.3$, $P=0.02$; Vespidae $t=2.1$, $df=63.72$, $P=0.03$). This suggests that social species have longer distances to other flower visitors (in number of direct interactions) than solitary species, indicating that they use distinct subsets of the flowering plants available.

In contrast to the results for species-level metrics, sociality was not associated with the network-level organisation of pollination networks (Fig. 4). The proportion of highly eusocial hymenopteran species (I_E) was negatively associated with levels of closeness centralisation and weighted modularity (model 3 selected, Table 2). However, the model that assumed no effect of proportion of social or highly eusocial species on network metrics (model 1) was also selected for these metrics (Table 2). For weighted nestedness and betweenness centralisation, only the null model (model 1) was selected (Table 2). These results are not likely to be due to differences in sampling effort between networks, since even if the proportion of social species does decrease with species richness, network-level metrics show no association with sampling effort (Supplementary material Appendix 1, Table A10, Fig. A1).

Discussion

The way in which species traits shape patterns of species interactions is fundamental to understanding the organisation of ecological networks (Sebastián-González et al. 2017). Here we demonstrate that sociality is one such a trait influencing species interaction patterns. We find that social flower visitors interact with more plant species that are highly dependent on them than do solitary species, and that social species are more connected to other species in the network by direct and indirect pathways. These patterns were significant despite the wide variation in the network roles of solitary species. We also show that within the species-rich families in Hymenoptera, social species only have important network roles within Apidae. The effect of sociality on the interactions of apid bees was mediated by the high interaction frequency of social Apidae species. Despite its influence on interaction patterns at a species-level, we found that sociality does not affect the metrics describing overall

network structure.

We provide empirical support for the ideas of Thompson (1982) by showing that social flower visitors, as opposed to solitary, are among the most important species within pollination networks from a range of latitudes. Despite being associated with lower values of PC2 (associated with closeness centrality), social species had high values of PC1 which was highly positively correlated with six out of seven species-level metrics, including degree, interaction strength, and weighted centrality. A within-family analysis revealed that only social members of the Apidae family had prominent network roles, suggesting sociality shapes interaction patterns of species in at least one of the most species-rich bee families. This points towards an interaction between sociality and evolutionary history in determining the network role of social Apidae species. In various other taxa, social behaviour is also a key factor driving the prominent role of the species within interacting assemblages. Group-foraging bird species for example, are important module connectors in seed dispersal networks (Schleuning et al. 2014). Group foraging increases the ability to detect resources (Beauchamp 1998), which in turn may increase the number of species eaten by birds. Social predators such as wolves and hyenas are often among the most highly connected species in their food webs (Sinclair et al. 2003, Yeakel et al. 2012, 2013). In mammalian predators such as these, social organisation allows the species to prey upon individuals which would normally be too large for an animal hunting alone (Macdonald 1983). Thus, sociality leads to an increase in the number of interactions at an individual level, and therefore to a higher number of interactions for the species as a whole.

Our work suggests that the high number of individuals within certain social species, may explain their important role in pollination networks. It has been hypothesised that the observed importance of eusocial species in pollination systems is

related to an increase in interaction numbers due to three key traits of eusocial species: a high number of individuals, perennial colonial activity and specialised foraging casts (Thompson 1982). If these three traits do indeed lead to an increasing number of interactions, we would expect highly eusocial species to be highly connected in mutualistic networks. Our results, however, do not support this prediction. Competing models which compared sociality *per se* with the different levels of sociality showed that species with increasing levels of sociality do not have more prominent network roles. The results suggest that having perennial colonies or specialised foraging castes may not be as important in promoting central network roles as previously thought. In contrast, the numerical effect of having several individuals living together, combined with behaviours such as group foraging (Lichtenberg et al. 2010), may explain why some social species are keystones of pollination networks.

One of the first steps in the evolution of sociality is communal nesting (Wilson 2000), an immediate consequence of which is the numerical effect of many individuals living together. Sociality is associated with interaction frequency of apid bees (Fig. 3c, f), and our path analysis show that the effect of sociality on the network roles of apid bee species is mostly indirect, mediated by species interaction frequency, while the direct effect of sociality is only marginally significant. This supports the idea that the numerical effects of sociality may explain the role of social species in pollination networks. Numerical effects, e.g. abundance based-effects, are known to be important in organising species interactions (Krishna et al. 2008, Vázquez et al. 2009, Suweis et al. 2013, Vizentin-Bugoni et al. 2014). We hypothesise that sociality shapes the role of social flower visitors in pollination networks by favouring large abundance of individuals. If this is the case, abundance should not simply be a matter of sampling, or a factor to be controlled for when investigating the biological correlates of network

organisation. Instead, abundance may be a result of traits that favour a species' ecological success (i.e. numerical effects are a consequence of other traits).

Our study demonstrated that the presence of social species does not affect overall network structure, as models assuming no effect of the proportion of (eu)social species on network metrics performed better or as good as models which treated the proportion of eusocial hymenopterans as an important factor. The ecological basis of structural patterns in mutualistic networks has been the subject of investigation in a number of studies (Rezende et al. 2007b, Guimarães et al. 2007b, Gómez et al. 2010, Donatti et al. 2011). Most patterns are robust to differences in species composition, environment or interaction types (Ollerton and Cranmer 2002, Bascompte et al. 2003, Vázquez and Aizen 2004, Guimarães et al. 2007a). The structure of ecological networks is also robust to temporal fluctuations in species abundance (Olesen et al. 2008, Dupont et al. 2009, Díaz-Castelazo et al. 2010, Rasmussen et al. 2013) and to species loss and rewiring of interactions (Kaiser-Bunbury et al. 2010, Aizen et al. 2012, Timóteo et al. 2016). This suggests that some aspects of network structure are shaped by general features of ecological systems, such as interaction intimacy (Guimarães et al. 2007b), patterns of niche overlap (Pires et al. 2011, Williams and Martinez 2000) or species abundance distributions (Krishna et al. 2008, Vázquez et al. 2009), and not by traits which are specific to particular ecological interaction types.

Our study is a step towards an understanding of how behavioural traits organise the role of species in ecological networks. Some social Apidae species (such as various *Apis* and *Bombus*) occupy important roles in pollination networks, but their presence does not change network organisation. This may be because in their absence other species expand to fill similar structural roles (see Timóteo et al. 2016 for an example on seed-dispersal networks). Future work should therefore investigate in more detail

the mechanisms driving species' roles in ecological networks, and the mechanisms shaping overall network structure. One of the key steps in understanding the role of social insects in pollination networks will be to accurately assess their efficiency as pollinators (Munyuli 2014). If social species at the core of pollination networks are efficient pollinators, for instance as a result of longer visits and greater pollen deposition (Munyuli 2014), their high abundance, wide phenology and specialised foraging castes should result in a reliable pollination service to many plant species. However, some abundant and highly connected flower visitor species, such as *Apis mellifera* (Linnaeus, 1758), can be poor pollinators when compared with other species (Ollerton et al. 2012, Nabors et al. 2018). In this case, plants could be receiving an inferior pollination service to that provided by more specialised insect species. Social, highly abundant insect species may dominate resources and promote high competition (Lichtenberg et al. 2010, Samnegård et al. 2014), pushing individuals of rarer species towards higher fidelity, thus increasing plant reproductive success (Brosi and Briggs 2013). Future studies should investigate the evolutionary implications of scenarios such as these in which central flower visitor species do not provide efficient pollination.

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Supplementary material (available online as Appendix oik-05387 at <www.oikosjournal.org/appendix/oik-02685>). Appendix 1.

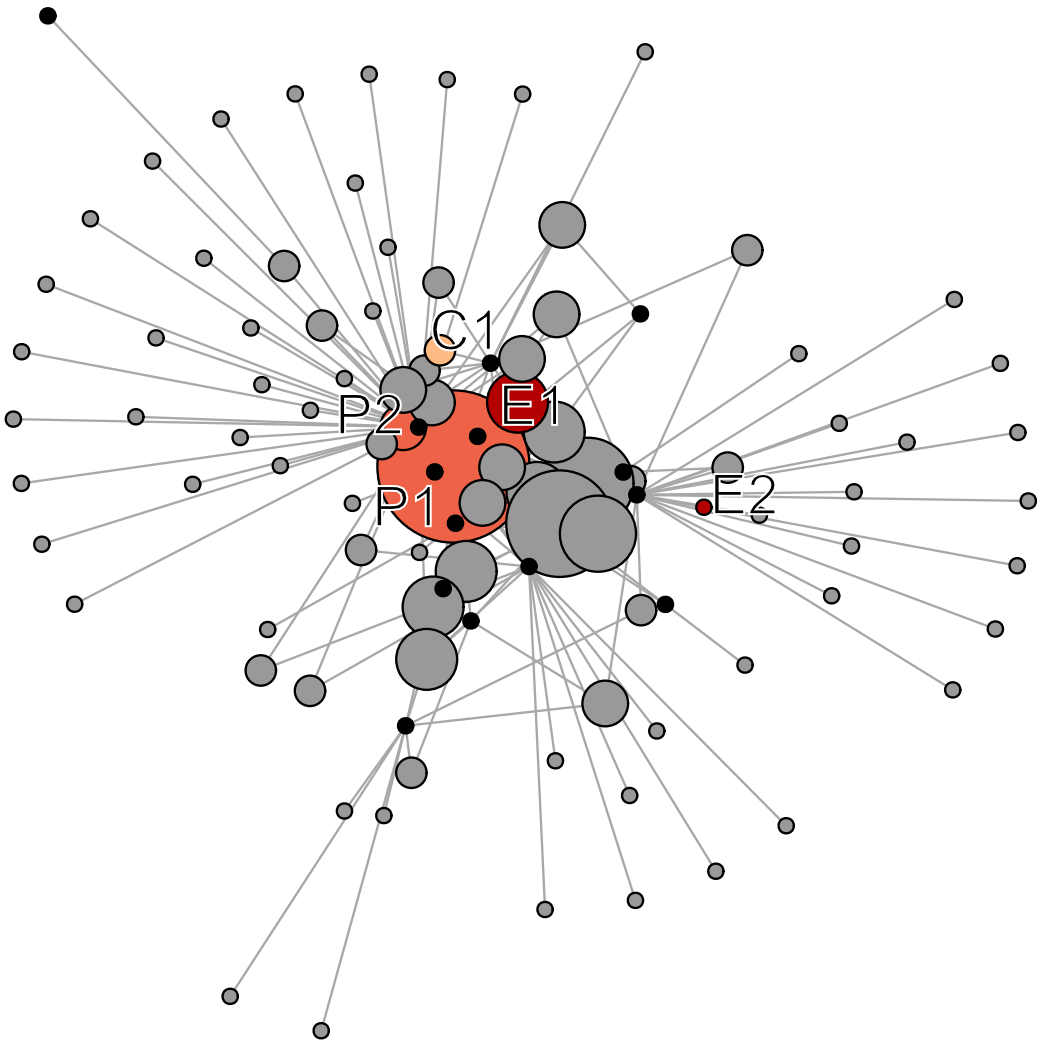

Figure 1. Pollination network from a montane forest in Argentina (Vázquez 2002). Nodes are plant and flower visitor species and lines are interactions. Plants are in black, solitary flower visitor species in grey and social species in shades of red: communal species in light red (C1 = Protandrena sp.), primitively eusocial species in medium red (P1 = Bombus dahlbomii, P2 = Bombus ruderatus) and highly eusocial species in dark red (E1 = Vespula germanica, E2 = Camponotus sp.). Size of nodes for flower visitors are proportional to species degree.

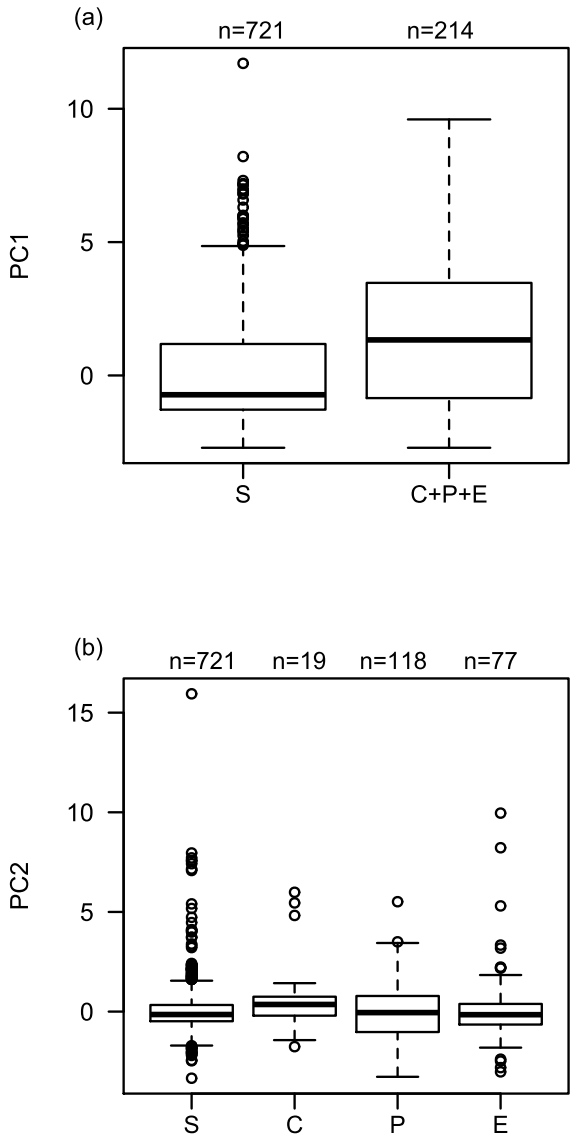

Figure 2. Boxplots of species-level metrics per level of sociality. a) PC1 of solitary versus social species (C, P and E combined); b) PC2 for each level of sociality (S, C, P and E). S=solitary, C=communal, P=primitively eusocial, E=highly eusocial.

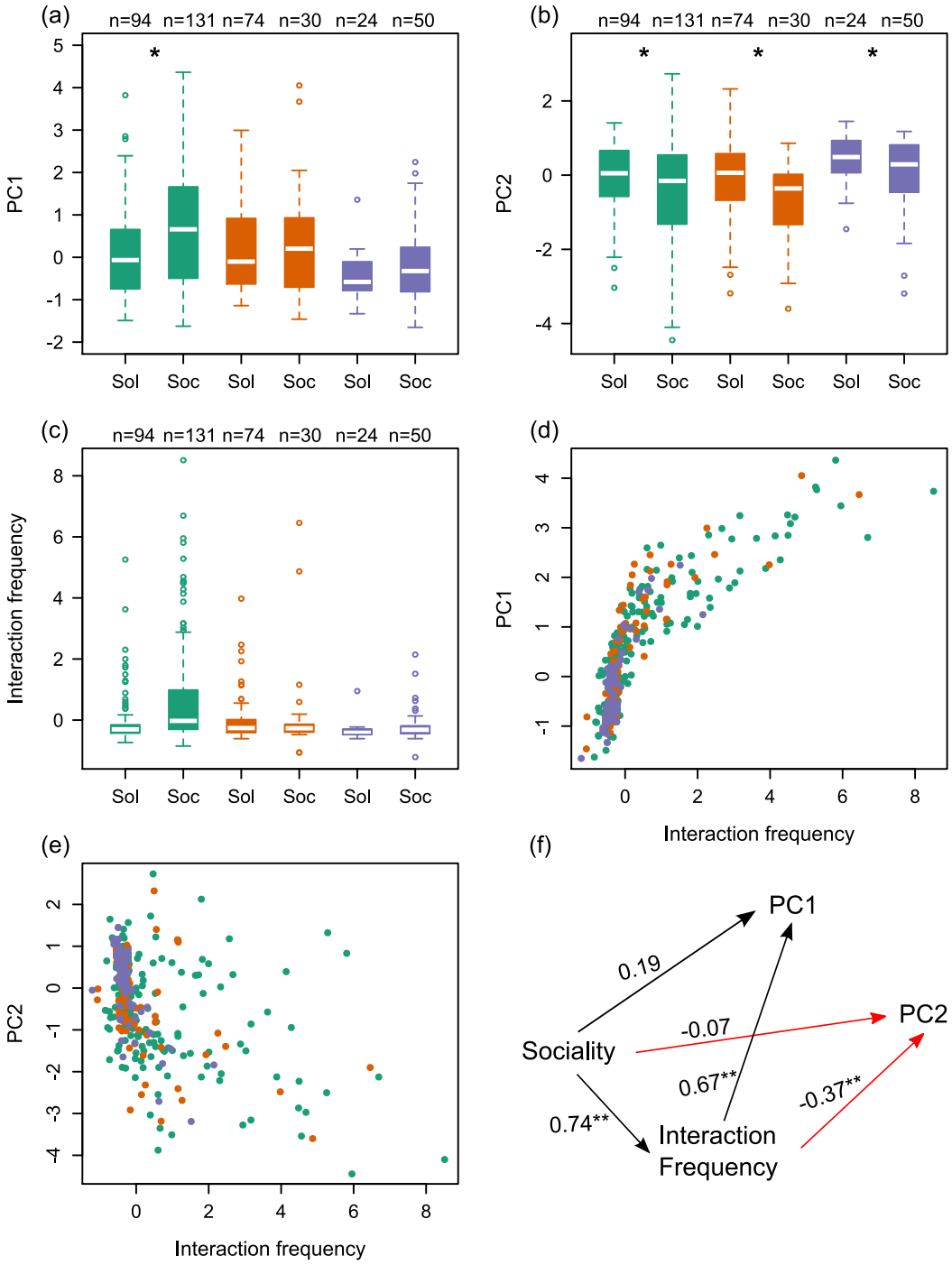

Figure 3. Values of a) PC1, b) PC2 and c) interaction frequency for social (C, P and E combined) and solitary species of Apidae (green), Halictidae (orange) and Vespidae (purple); relationship between d) PC1 and e) PC2 and interaction frequency, each dot is a species of the families Apidae (green), Halictidae (orange) and Vespidae (purple); f) diagram of the effects of sociality (C, P and E combined) on interaction frequency, PC1 and PC2 of Apidae species, black arrows are positive and red arrows are negative effects. In all plots, values of PC1, PC2 and interaction frequency were *Z*-scored inside each network. C=communal, P=primitively eusocial, E=highly eusocial.

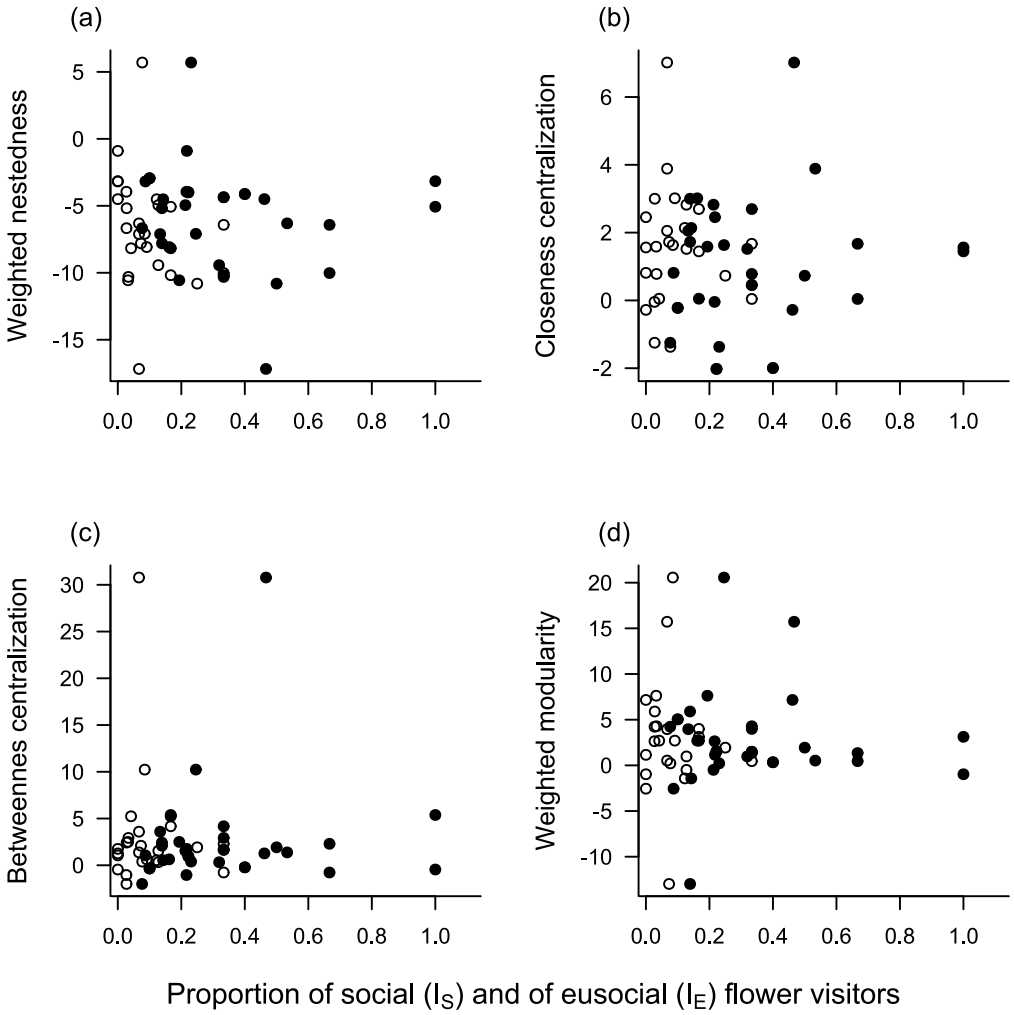

Figure 4. Relationship between the proportion of social and of highly eusocial hymenopteran species and network-level metrics. Closed circles represent the proportion of social hymenopteran species (I_S), and open circles the proportion of highly eusocial hymenopteran species (I_E). Network-level metrics were *Z*-scored: a) weighted nestedness, b) closeness centralisation, c) betweenness centralisation, and d) weighted modularity.

Table 1. Models for the effect of sociality on species network roles (PC1 and PC2) in the first and second round of analysis. In the first round, the four competing models had as fixed effects: no explanatory variable (model 1), sociality (model 2), sociality and interaction frequency (model 3) and interaction frequency (model 4). In models 2 and 3, sociality was divided into two levels (2LSoc): solitary versus social (C, P and E combined) species. In the second round, the selected models (model 3 for PC1 and model 2 for PC2) competed with one additional model each (model 3.b for PC1 and model 2.b for PC2) with a similar structure of the selected models but with sociality split into four levels (4LSoc): S versus C versus P versus E. S=solitary, C=communal, P=primitively eusocial, E=highly eusocial. Selected models (ΔAIC < 2) are shaded. AIC = Akaike's Information Criterion and ΔAIC = AIC of each model – AIC best model.

First round of analysis

Competing models	**Fixed effects**	**PC1**		**PC2**	
		AIC	**ΔAIC**	**AIC**	**ΔAIC**
Model 1	_____	4188.1	182.3	2120.8	35.5
Model 2	2LSoc.	4112.2	106.3	2085.2	0.0
Model 3	2LSoc.*IntFreq.	4005.9	0.0	2118.8	33.6
Model 4	IntFreq.	4141.3	135.5	2138.3	53.1
Second round of analysis – PC1					
Model 3	2LSoc.* IntFreq.	4005.9	0.0		
Model 3.b	4LSoc.* IntFreq.	4022.2	16.3		
Second round of analysis – PC2					
Model 2	2LSoc.			2085.2	6.1
Model 2.b	4LSoc.			2079.1	0.0

Table 2. Models for network-level metrics weighted nestedness (wNODF), closeness (CC) and betweenness centralisation (BC) and weighted modularity (Q). The three competing models had no explanatory variable (model 1), proportion of social hymenopterans (I_S) as explanatory variable (model 2), proportion of highly eusocial social hymenopterans (I_E) as explanatory variable (model 3). Selected models ($\Delta AIC < 2$) are shaded. AIC = Akaike's Information Criterion and ΔAIC = AIC of each model – AIC best model.

		wNODF		**CC**		**BC**		**Q**	
Models	**Exp. Var.**	**AIC**	**ΔAIC**	**AIC**	**ΔAIC**	**AIC**	**ΔAIC**	**AIC**	**ΔAIC**
Mod. 1	_____	166.7	0.0	122.5	0.0	188.6	0.0	186.5	0.0
Mod. 2	I_S	168.8	2.2	124.6	2.1	190.7	2.1	189.0	2.5
Mod. 3	I_E	169.0	2.3	122.8	0.3	190.8	2.2	188.4	1.9